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ORIGINAL PAPER

Evolutionarily Stable Relocation Strategy in an Antlion Larva

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Abstract Antlion pits are often spatially aggregated even though there are potential negative effects associated with the aggregation (e.g., heightened competition and predation risk). This study investigated the possibility that a strategy leading to aggregation can be an evolutionarily stable strategy (ESS). In particular, the strategy considered was 'decreasing relocation tendency when there are neighbors'. An individual based model showed that the strategy can be the unique ESS when the spatial distribution of prey is not completely random and antlions can learn it from their past foraging experiences. A laboratory experiment was conducted to examine the effects of the presence of neighbors and foraging success on the relocation behavior of antlion larvae. Antlions reduced their relocation tendency with respect to these factors, consistent with the predicted ESS. The results suggest that pit aggregations are formed because antlions reduce their relocation tendency when neighbors exist, and this strategy is an ESS.

Keywords Evolutionarily stable strategy · relocation · social information · *Myrmeleon persimilis*

Introduction

The success of organisms that forage around a fixed point such as central place foragers (Orian and Pearson 1979) and trap foragers are strongly influenced by the quality of their foraging locations. To address this issue, these foragers relocate when their foraging sites are not suitable (Sharpe and Millar 1990; Gordon 1992; Lubin et

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al. 1993). For example, many species of antlion larvae (Neuroptera: Myrmeleontidae) are sit-and-wait predators that build conical pit traps in fine particulate substrates to capture mobile invertebrates (Wilson 1974; Heinrich and Heinrich 1984; Crowley and Linton 1999). It is important for antlions to select profitable locations for constructing their pits (Wilson 1974; Riechert 1976; Hart 1987; Scharf et al. 2011). Antlions must evaluate their current locations and relocate to others if the sites are found unsuitable. In this study, we examined antlion larvae as an example of trap foragers.

There are a number of known factors that affect pit relocation behavior in antlion larvae (see Scharf and Ovadia 2006 for review). Among physical factors, temperature (Klein 1982; Lucas 1989; Gotelli 1993; Arnett and Gotelli 2001), light intensity (Klein 1982; Scharf et al. 2008a; Scharf et al. 2008b), rainfall (Gotelli 1993; Morrison 2004), and soil moisture (Heinrich and Heinrich 1984) are known to be important. In addition, properties of sand particles are also crucial. Antlions generally build pits in sandy habitats with fine grained particles (Farji-Brener 2003; Devetak et al. 2005). Particle size affects pit characteristics (e.g., size, depth, and angle) that influence prey capture success (Burgess 2009; Devetak et al. 2012).

Although the physical factors are considered the primary factors constraining the spatial distributions of antlion pits (Gotelli 1993; Morrison 2004; Scharf et al. 2008a), biotic factors also influence pit relocation behavior. Starvation (e.g., influenced by prey availability) triggers relocation (Hauber 1999; Arnett and Gotelli 2003; Scharf et al. 2009), but responses to starvation are variable among species, and direct evidence linking prey availability and pit site selection in the field is scarce (Scharf and Ovadia 2006). Predation is also considered as an important factor. Predators of antlions include antlions themselves (i.e., intraguild predation and cannibalism) (Griffiths 1991; Griffiths 1992; Barkae et al. 2010). Antlions can recognize and respond to different predator types (i.e., active predator vs. sit-and-pursue predator) in making relocation decisions (Loria et al. 2008). These factors many not act independently; an interaction between starvation and predation risk (e.g., trade-off) also influences the foraging behavior of antlions (Tsao and Okuyama 2012).

Competition is also an important biological interaction that affects antlions. In particular, shadow competition can be strong among antlion larvae (Wilson 1974). In shadow competition among antlions, pits located in “upstream” (prey move from upstream to downstream) can intercept prey paths, thus ones located “downstream” will experience reduced prey intake (Linton et al. 1991). Despite the potential importance of shadow competition, there is no consensus about how antlions respond to the density of competitors (McClure 1976; Simberloff et al. 1978; Griffiths 1992). Thus, one puzzling but common observation is that antlion pits are often found in aggregations (Gotelli 1993), which would enhance the intensity of shadow competition as well as predation risk (e.g., cannibalism). Although these biological factors are known to influence relocation behavior, little is known about how they translate to the formation of spatial pit distributions.

One factor that may link the biological factors and the formation of pit aggregations is social information. In particular, inadvertent social information has been increasingly considered important in the assessment of patch quality (see Blanchet et al. 2010 for review). Inadvertent social information can be any perceivable cues where individuals that produce cues do not intend the cues to be used as information by others. For example, prey often exhibit antipredator behavior when encountering a predator (e.g., fleeing). Other individuals that have not detected a predator may learn about the danger by seeing the antipredator behavior exhibited by others (Ferrari et al. 2005). The use of inadvertent social information is taxonomically widespread (Galef and Giraldeau 2001; Danchin et al. 2004; Dall et al. 2005; Blanchet et al. 2010; Rieucau and Giraldeau 2011), but its importance in the relocation behavior of antlions has not been studied.

With respect to the pit site selection of antlions, inadvertent social information can be the mere presence of neighboring conspecifics. Antlions relocate if their current locations are not suitable. Then, the presence of antlions would indicate that the quality of the location is good. Antlions can detect the presence of conspecifics at least in two ways. Antlions toss sand particles outside their pits, e.g., for maintenance (Youthed and Moran 1969; Lucas 1982; Griffiths 1986), and sand particles often enter the pits of neighboring antlions (Heinrich and Heinrich 1984). Thus antlions are likely to be able to detect the presence of neighboring antlions without directly encountering each other. In addition, antlions are highly sensitive to mechanical vibratory cues propagated in sand (Devetak et al. 2007; Fertin and Casas 2007; Hill 2009). Thus, even without sand particles tossed from other pits, antlions may be able to perceive other antlions through vibratory cues.

In this study, we examined the role of social information in pit relocation behavior. In particular, we examined whether a strategy that leads to aggregations (i.e., *decreasing relocation tendency when neighbors exist*) can be an evolutionarily stable strategy (discussed below). First, we show that the strategy can be an evolutionarily stable strategy by using an individual based computer model. Simulation models are useful in examining complex systems (e.g., interaction between spatial and behavioral factors) whose mathematical approximations are not obvious (Okuyama 2008; Okuyama 2009; Scharf et al. 2012). After the establishment of the theoretical result, we empirically show that the antlion, *Myrmeleon persimilis*, exhibits relocation behavior that is consistent with the theoretical evolutionarily stable strategy.

Individual Based Model

An individual based model (IBM) that simulates a scenario where multiple antlions forage in a common environment was created. In the scenario, each antlion has a relocation strategy (i.e., how neighbors influence its relocation tendency). The model runs in discrete time by iterating a few procedures. In below, the order in which the procedures are executed is described first, and then the definitions of the procedures are described in detail.

Simulation steps

1. Initialization (execute *Environment procedure*)
2. Check the identity (ant or antlion) of each existing individual in a random order
    a. If the individual is an ant, execute *Ant procedure*
    b. If the individual is an antlion, execute *Antlion procedure*
3. A new ant may be introduced (execute *Ant entrance procedure*)
4. Repeat Step 2 and Step 3 for N_{SIM} time steps

Environment Procedure

The model is a two-dimensional spatially explicit model. The environment is a square (101×101 units). The coordinate of the center of the environment is (0,0). The four corners of the environment are (−50.5,50.5) [top-right], (50.5,50.5) [top-left], (−50.5,−50.5) [bottom-right], and (50.5,−50.5) [bottom-left]; thus, the length of one side is 101 units as described. The model is point-process based in which organisms (ants and antlions) can be located at any point in the environment. However, antlions are restricted within a circular area (e.g., representing a sandy habitat) whose radius is 50 units centering at (0,0). Antlions cannot move outside the circular area. The locations of antlions at the beginning of a simulation are randomly chosen within the circular environment.

Ant Procedure

Ants exhibit correlated random walk. Each ant has its own heading direction that changes at each time step. Suppose that the current heading angle is θ_C. At each time step, the new heading direction is determined as $\theta_{NEW}=\theta_C+U_1+U_2$ where U_1 and U_2 are random numbers generated from the uniform distributions whose domains are $(0,\theta_A)$ and $(-\theta_A,0)$, respectively. θ_A is a parameter that determines the tendency for an ant to move straight. For example, when $\theta_A=0$, ants do not change the heading direction at all. In each time step, ants move forward for a specified distance determined by a parameter, d_A. When an ant moves outside the square environment, the ant does not reenter the environment. When an ant enters a pit of an antlion, the ant is eaten by the antlion.

Antlion Procedure

Although the number of antlions can be set arbitrarily in the model, we considered an environment with two antlion larvae to simplify the scenario. Each antlion can be in one of the two states: stay state or relocation state. When an antlion is in a stay state, the antlion stays at the current location with a pit whose diameter is π. If an antlion is in a relocation state, it moves within the circular environment for T_R time steps. The movement details follow those of ants described above, but antlions have own parameters, i.e., θ_L and d_L. When an antlion that is in the middle of relocation enters the pit of the other antlion, it will change the heading angle to escape from the pit (no cannibalism is possible). Suppose an antlion steps into a pit and the direction (i.e., angle) of the pit owner is θ_O, then the new heading angle will be θ_O+W where W is a random number generated by a uniform distribution whose domain is (90,100) with the probability 0.5 or (−100,−90) with the probability 0.5. Lastly, it is assumed that the pits of two antlions do not overlap. Thus, at the end of a relocation state, if an antlion that is about to make a new pit is too close to the other antlion, its relocation state extends until it reaches a location where the two pits do not overlap.

The transition from a relocation state to a stay state is deterministic as described above. The transition from a stay state to a relocation state depends on an antlion's experience at the current location and is probabilistic. Suppose that an antlion just entered a stay state, the antlion stays at the current location at least for T_S time steps.

After T_S time steps, whether the antlion relocates or continues to stay is determined by its prey capture success during the T_S time steps. At the beginning of a stay state, two internal perception variables (h and m) of an antlion are (re)set to 0 (i.e., $h=m=0$). Both variables change based on foraging success. In each time step, when an antlion captures an ant, h and m change according to Eq. (1), and when it fails to capture a prey, the variables change according to Eq. (2),

$$h_{\mathrm{t}+1} = \rho h_{\mathrm{t}} + 1 \quad \text{and} \quad m_{\mathrm{t}+1} = \rho m_{\mathrm{t}}, \tag{1}$$

$$h_{\mathrm{t}+1} = \rho h_{\mathrm{t}} \quad \text{and} \quad m_{\mathrm{t}+1} = \rho m_{\mathrm{t}} + \exp(\kappa x), \tag{2}$$

where the subscript represents the discrete time step. The parameter ρ describes the memory retention rate. When $\rho=1$, antlions do not forget previous experiences. κ describes the effect of neighboring antlions, and x is the number of the neighbors. Two antlions are considered neighbors to each other if the distance between them is less than δ. In this study, because there are only two antlions, x is either 0 or 1. When antlions are adjacent to each other, they will enforce immediate shadow competition. This is because an ant that was going to be fall into the pit of an antlion can be intercepted by the adjacent antlion.

In Eqs. (1) and (2), an antlion increases h when it captures a prey and increases m when it does not capture a prey. Thus, h relates to positive experience, and m relates to negative experience at the current pit location. Furthermore, how an unsuccessful prey capture influences m depends on one's strategy, described by κ. Assuming $\rho=1$ (because it is easier to describe how to interpret κ, but the general interpretation will be the same for other ρ values), when there is no neighbor ($x=0$), m increases by 1 regardless of κ if an antlion does not capture a prey. However, when there is a neighbor ($x=1$), m increases by more than 1 ($\kappa>0$), by 1 ($\kappa=0$), or by less than 1 ($\kappa<0$). In other words, when $\kappa=0$, neighbors do not influence the perception of an antlion. However, when $\kappa<0$ or $\kappa>0$, an unfavorable experience (i.e., no prey capture) is discounted or amplified by the presence of neighbors. For simplicity, we assumed the possible values of κ to be −1, 1, or 0, resulting in three strategies, where neighbors discount, amplify or have no effect on unfavorable experience.

Each antlion uses its own h and m to evaluate the current pit location. Considering h (prey capture) and m (no prey capture) as outcomes of a binomial process (e.g., h successes in $h+m$ trials), an antlion's perception about the probability of prey capture can be described as Beta($1+h$, $1+m$) if we assume that naïve antlions perceive that the probability of prey capture can be any value between 0 and 1 (i.e., uniform distribution), according to a Bayesian information updating (Gelman et al. 2004; Dall et al. 2005). At the end of a stay state, a random variable is generated from Beta($1+h$, $1+m$), representing how an antlion perceives the quality of the current pit location in terms of the prey capture probability. If the value is less than a threshold value ϕ, it relocates. If the value is greater than ϕ, it continues a new stay state at the current location. Therefore, when $\kappa=-1$, transitions to a relocation state are less likely when there is a neighbor because unfavorable perception m increases slowly. On the other hand, when $\kappa=1$, antlions are more likely to relocate if neighbors exist because of the enhanced m.

Ant Entrance Procedure

New ants enter the environment at a given time interval τ. For example, when $\tau=500$, a new ant is introduced every 500 time steps. Ants come into the environment from one of the four corners. The entrance corner randomly changes at a specified time intervals λ. For example, suppose $\lambda=1000$ and $\tau=10$, then a new ant enters every 10 time steps for 1,000 time steps only from one of the four corners because the entering corner does not change for 1,000 time steps. In this example (i.e., $\tau=10$), suppose $\lambda=5$, the corner a new ant enters is randomly chosen for each ant. Thus, the larger λ is, the more predictable where new ants come from; λ is considered environmental predictability. When a new ant is introduced, its initial heading direction is randomly chosen from a uniform distribution whose domain in the angles of the two adjacent corners (90°). The simulation model was built using NetLogo (Wilensky 1999).

Analysis

Each antlion has a fixed κ as its strategy. We assume that κ is heritable, and foraging success (i.e., number of prey captured) is an appropriate surrogate of fitness. Then κ^* is an evolutionarily stable strategy (ESS), when $s_1=s_2=\kappa^*$ (s_1 and s_2 are the values κ used by two antlions), changing to another strategy will reduce the fitness. Many outcomes are possible (e.g., no ESS, every strategy is an ESS). In this study, we focused on finding the condition where $\kappa=-1$ (i.e., reducing relocation tendency when neighbors exist) is the only unique ESS because this result most closely ties to the ubiquitous pit aggregations in the field. One simulation run consisted of 500 000 time steps (N_{SIM}). Because each antlion can have one of the three strategies, there are nine possible combinations between two antlions.

To examine the effects of memory ρ and environmental predictability λ, the values of these parameters were also varied (Table 1). All possible factorial combinations of the parameters were examined, and for every parameter combination, 300 replications

Table 1 Parameters of the individual based model, their definitions and default values

Definition	Symbol	Value
Environmental predictability	λ	100, 100000
Ant entrance interval	τ	100
Stay interval	T_S	250
Relocation interval	T_R	250
Memory	ρ	0.1, 0.3, 0.5, 0.7, 0.9
Relocation threshold	ϕ	0.1
Neighbor effect	κ	−1, 0, 1
Antlion movement distance	d_L	20
Ant movement distance	d_A	10
Antlion heading angle	θ_L	10
Ant heading angle	θ_A	10
Pit diameter	π	16
Neighbor distance	δ	20

When multiple values are shown, all the possible factorial combinations were examined were conducted. Because this is a computer simulation study, it is possible to increase the sample size arbitrarily. Thus, discussing statistical significance may be of little value (Johnson 1999). Nonetheless, in order to indicate patterns observed in the limited number of simulation runs are not due to random chance, statistical significance was also examined.

Laboratory Experiment

Study Animals

We collected *Myrmeleon persimilis* larvae from coastal habitats in Shimen District, New Taipei City (25°18′N, 121°32′E). It is a sandy region with abundant rainfall. When it rains, *M. persimilis* larvae burrow few centimeters under the sand surface (directly beneath the original pit site) and come out when the sand is dry. The common plant species in the habitat include wormwoods (*Artemisia capillaries*), tree heliotropes (*Tournefortia argentea*), Hosobawadan (*Crepidiastrum lanceolatum*), and Indian Blankets (*Gaillardia pulchella*) (personal observations). Antlions used in the experiment were individually housed in plastic trays filled with sands (44.5 cm×34.7 cm, sand depth 4 cm) maintained in a controlled environment: temperature (25±2 °C), relative humidity (40±5 %), and L:D 14:10 cycle. Because pits are small (≈ 2 cm in diameter) (Tsao and Okuyama 2012), the trays were considered sufficiently large for this study. Sand used in the study was collected from the same location where antlions were collected.

Effects of Prey Supply and Sand Tossing on Relocation

This experiment examined whether prey capture success and the presence of neighbors influence relocation behavior. We used a 2×2 factorial design in which prey capture success (two levels: no prey vs. one prey per day) and sand tossing (two levels: no sand tossing vs. sand tossing per day) were manipulated. Flour beetle larvae, *Tribolium confusum*, were used as prey. The sand tossing treatment was intended to mimic the sand tossing behavior of antlions (see Introduction) in which 0.25 ml of sand was introduced to a pit four times (2 s interval between each introduction). A plastic tube was used to make sand slide down into a pit. These details were decided based on preliminary observations on sand tossing behavior. In the experimental group that received both treatments, antlions received a prey first. After the prey was consumed, the sand tossing manipulation was performed. The treatments were applied daily for 1 month, and relocations were recorded daily. All the manipulations and recordings were done between 1530 and 1730.

Statistical Analysis

The effect of the treatments on the propensity to stay at the same initial location was examined using Cox's proportional hazard analysis. The model relates durations to the first relocation event and the treatments. Some individuals did not relocate at all during the experiment (i.e., 30 days), and those observations were used as censored data. The two factor variables were used as the explanatory variables. Using the model selection method based on the Akaike Information Criterion (AIC) (Akaike 1973), the relationship between the treatments and durations antlions took to relocate was examined.

The relationship between the treatments and the number of relocations was also examined. Because relocation events were observed daily for 30 days, the number of relocations was modeled as a binomial process using Generalized Linear Mixed Model (GLMM). Because each individual was repeatedly measured for 30 days, the random intercept and the random time effect accounting for the repeated measurements were also included. The explanatory variables considered were the same as the previous analysis. However, in addition, time was also entered as an explanatory variable. The best model was chosen based on AIC. The parameter estimates of the best model are presented based on the restricted maximum likelihood (Zuur et al. 2009). All statistical analyses were conducted in R (R Development Core Team 2012).

Results

Individual Based Model

Because there are three strategies ($\kappa=-1$, 0, and 1) and two individuals, there are nine possible pairwise combinations when we allow each strategy to compete against each other. The nine points (i.e., simulation results) are shown in each figure panels (Fig. 1). The strategy leading to aggregation ($\kappa=-1$) is the unique ESS when antlions have sufficient memory (i.e., $\rho\geq0.7$), and the environment is not highly variable (i.e., $\lambda=100\,000$) (Fig. 1). This is because regardless of the opponent's strategy ($\kappa=-1$, 0, or 1), the aggregation strategy ($\kappa=-1$) always resulted in the highest energy gain. In these conditions, individual fitness decreased as κ increased (Kendall's tau, $p<0.05$ for all cases). In the other scenarios, $\kappa=-1$ can still be an ESS, but other strategies can also be ESSs (Fig. 1), thus it is not the unique ESS.

Effects of Prey Supply and Sand Tossing on Relocation

The largest number of antlions (14 out of 15 individuals) relocated when they received neither prey nor sand tossing. Fewer individuals relocated in the other experimental groups (i.e., 12 individuals [prey only], 9 individuals [sand tossing only], and 12 individuals [prey and sand tossing]) (Fig. 2). Based on AIC, the best model is the model that includes only the sand tossing effect (Cox's proportional hazard model: sand tossing treatment coefficient=−0.66). The negative sand tossing effect indicates that the treatment decreased the likelihood of relocation.

Some individuals relocated multiple times during the experiment (Fig. 3). The best model (Binomial GLMM, [fixed effects] intercept=−1.428, prey=−0.722, sand=−0.482, time=−0.069; [random effects in terms of variance] intercept=0.051, time=0.002) indicates that antlions relocated less when they received prey and sand tossing (i.e., the parameter values are negative), but there is no interaction between the two treatments. The negative time coefficient of the model indicates that the probability of relocation also decreased with time.

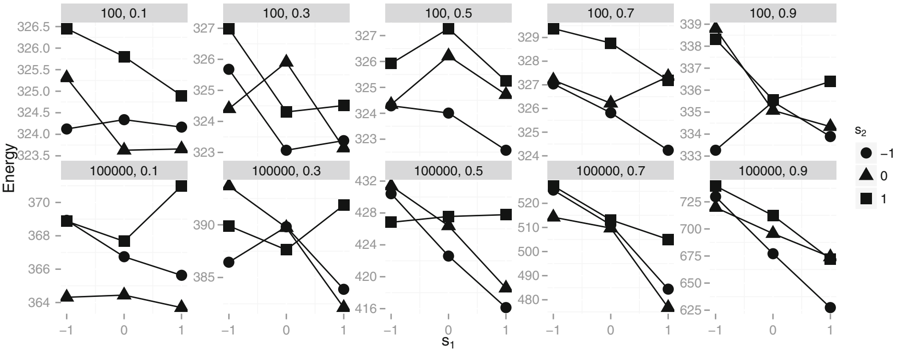


Fig. 1 Average number of prey (energy) captured by antlions at the end of a simulation run. The strategy of the focal individual is s_1, and the opponent's strategy is s_2. The two numbers in the panels indicate λ (100 or 100000) and ρ (0.1, 0.3, 0.5, 0.7, 0.9)

Discussion

The individual based model showed that a strategy leading to the formation of pit aggregations (i.e., relocate less when there are neighbors, $\kappa=-1$) can be evolutionarily stable. In the experiment, antlions decreased the number of relocations with respect to both the prey supply and sand tossing treatments (Fig. 3), and the effect of the prey supplement was stronger. This result suggests that antlions use their own experience (i.e., prey capture) as the primary source of information to make their relocation decisions but still use the social information (i.e., sand tossing) in a lesser degree to reduce uncertainty about the environment, consistent with how the decision making process was modeled in the individual based model as well as the predicted ESS. These results suggest that commonly observed spatial aggregation of pits may be partly due to their game theoretical interactions based on the use of the inadvertent social information.

In order for the strategy ($\kappa=-1$) to be the unique ESS, environment must be relatively predictable (i.e., high λ). In the model, inadvertent social information is the

Fig. 2 Proportion of larvae remaining at the initial locations. Sample size is 15 for each treatment combination

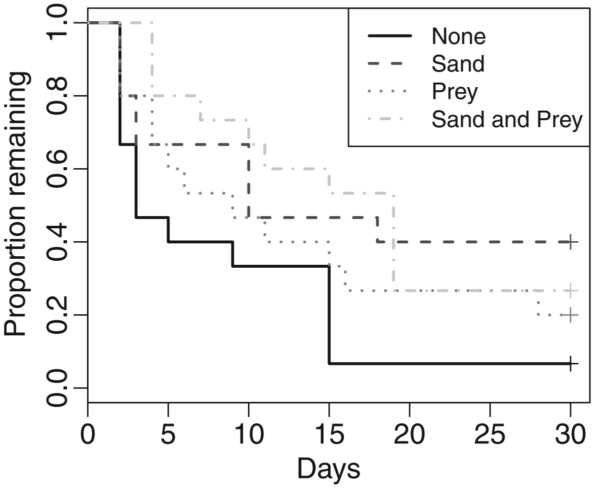
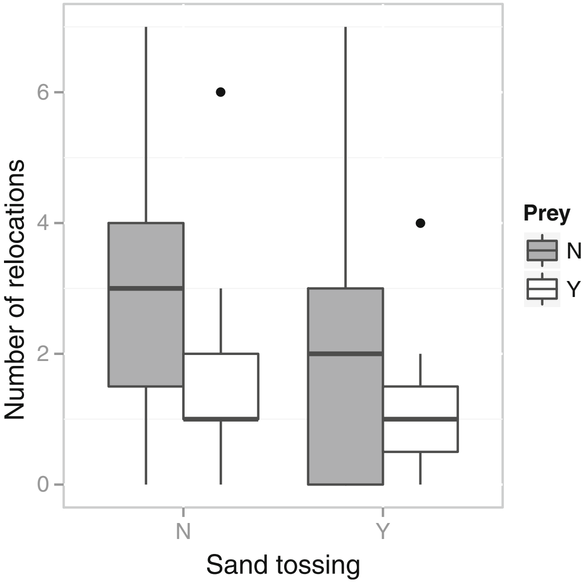


Fig. 3 Boxplots of the number of relocations in 30 days. Each treatment combination contains 15 replications. Y(es) and N(o) indicate the presence and absence of the treatments, respectively



mere presence of another antlion. Thus, in order for the location of an antlion to provide information about the quality of its location, each antlion must be able to track the environment by itself (i.e., in the absence of conspecifics). If the prey availability of a location is randomly determined (i.e., low λ), there is no location that is consistently better than other locations. Another important parameter is the learning ability of antlions. The model suggests it must be high (i.e., high ρ). This result also can make an intuitive sense. Even if some locations provide more prey, antlions would randomly relocate if they cannot learn. In nature, spatial patterns (e.g., patterns that cannot be described by Poisson distributions) are widely recognized (Bjørnstad et al. 1999; Koenig 1999; Ettema and Wardle 2002; Amarasekare 2003), and learning behaviors in insects are well documented (Dukas 2008; Guillette et al. 2009). Thus, the conditions (for $\kappa=-1$ to be the unique ESS) indicated by the model are likely satisfied in antlion populations.

In the model, an antlion pit is simply modelled as an area around a fixed point. Therefore, the model and its results are also applicable to other trap froagers and central place foragers. The study may have important implications as to why some predators aggregate despite the potential negative effects associated with aggregation. For example, jumping spiders are central place foragers where they forage around their nests but sometimes relocate to different locations (Okuyama 2011). Despite the frequent occurrence of intraguild predation and cannibalism among jumping spiders (Okuyama 2007), their nests are often found in high density (Okuyama 2011). Extremely high density of trap foraging (web) spiders are also commonly observed (e.g., Enders 1973; Miyashita 1992; Jakob et al. 2011). Although the idea that the presence of conspecifics reveals habitat quality is not new (Blanchet et al. 2010), it may also have an important role in the formation of extremely high densities of some predator groups.

Although shadow competition is included in the model, only two individuals were simulated whereas in the field aggregations can be formed by many individuals

(Gotelli 1993). Perhaps, the small number of individuals may have made the intensity of shadow competition weak in the model, but existing studies provide an alternative view. Web spiders, for example, would experience similar shadow competition where individuals in downstream (e.g., surrounded by other webs) receives reduced prey. However, insect prey may ricochet off outer webs and land on inner webs (Uetz 1989; Rao 2009), an effect called 'ricochet' effect (but see, Leborgne et al. 1998). Similarly, antlions in the inner aggregation may not receive fewer prey than ones located peripheral as often assumed in shadow competition. In fact, antlions experience unsuccessful prey encounters and respond to such events in specific ways (Scharf et al. 2010). Although, a ricochet effect has not been demonstrated in antlions (Scharf and Ovadia 2006), it is certainly an important effect to be examined.

An important caveat of the study is the interpretation of the sand tossing treatment. It has been suggested that antlions can perceive cues from sand tossing events as social information (Simberloff et al. 1978). However, this detail must be confirmed with further experiments. For example, the sand tossing manipulation used in the experiment may be perceived as cues from prey although they were intended as cues from conspecifics (Guillette et al. 2009). In addition to sand tossing, as discussed above, antlions are likely to be able to detect the presence of conspecifics via vibratory cues (Fertin and Casas 2007). While not much is known, other cues such as chemical cues may be used to detect neighbors. How antlions detect the presence of conspecifics and to what degree they can infer the density of conspecifics must be examined. Another caveat is the lack of simultaneous consideration of abiotic factors and biotic factors. While the current study focuses solely on a biotic factor, we already know abiotic factors strongly influence the pit site selections of antlion larvae (see Introduction). We need field studies examining how both factors contribute to the distribution of antlions. For example, by quantifying the availability of suitable microhabitats (in terms of abiotic factors) around aggregations of antlion larvae, we would know how strongly abiotic factors limit their distribution, which will allow us to tease apart the relative importance of biotic and abiotic factors.

Our study suggests that antlions decrease relocation tendency when neighbors exist, and this strategy may be an evolutionarily stable strategy. Although antlions do not form aggregations cooperatively, the ESS leads to aggregations because each individual is less likely to relocate when it is close to other individuals. Furthermore, because antlions still use their own experience as the primary information, they would not be trapped at poor locations simply because of (potentially misleading) social information. Given the results, it is important to validate some details of the model in future studies. For example, although Bayesian information updating was used in the model (Dall et al. 2005), little is understood how antlions update their perceptions towards environments as they gain experience. As decision making processes are the key in the aggregation phenomenon, detailed examinations of them would provide useful insights to the social interactions among predators.

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